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# Similarities, differences and mechanisms of climate impact on terrestrial vs. marine ecosystems

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## Abstract

Comparisons between terrestrial and marine ecosystems are generally not in the main stream of scientific literature even though Webb (2012) listed several points for which the transfer of knowledge and concepts related to one or to the other system would benefit our understanding of both. Even sharing this view, the leading hypothesis behind this contribution is that the pelagic system, where the dominant biotic component by number and biomass is microscopic, has specific features which strongly differentiate it from the above-the-surface terrestrial systems. Due to this, climate change, i.e. changes in temperature, precipitation and most importantly in the dynamics of the two fluid media, atmosphere and ocean, act with different mechanisms which prevents proceeding with analogies in many cases. In addition, the non-linearity of most of the processes and responses to perturbations requires, in order to obtain reliable forecasts or hindcasts, a detailed analysis of the path followed by the system which is normally overlooked in the step-change simulations or projections.

## Keywords

terrestrial, marine, climate change impact, LTER

## Background

Organisms, communities and ecosystems are continuously exposed to variations of weather components, namely, solar radiation, temperature, atmospheric pressure, humidity, cloud coverage, precipitation, wind speed and direction. These variations may

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be significant over the short natural cycles of daily and seasonal periods. However, their medians and the squared deviations around the median over a few decades are generally constrained within narrow intervals for each specific geographic location. Those characterise the climate of the specific site (IPCC 2007, IPCC 2013). Therefore climate is just the emergent pattern of weather variations in a specific site over a few decades. If the values, mentioned before, change systematically beyond the typical ranges then, by definition, a climate change is taking place. This raises the question of why climate change, which is a persistent change of the median values of weather components, generally lower than the short term variance of weather variability, has a significant impact on ecosystems.

The weather components listed above are all abiotic processes/variables of the atmosphere or the sun. The reciprocal feedback between abiotic atmospheric processes and biota has been well established in the last decades (IPCC 2013) but, by tradition, we still speak of climate forcing and ecosystem response. The reason may be that three of the key processes that affect the climate system, the radiation emission by the sun, directly and the earth rotation and tectonics, *sensu lato*, indirectly, are substantially out of the control of biota.

Considering the above definition of climate, another question arises: is a significant climate change presently going on? Recalling the previous statements, climate change means that the weather/climate variables display a persistent change in space and time at regional and global scales. This has always occurred in the past. Primarily because of the orbital coupling of sun-earth system whose main manifestation are the Milankovitch cycles (Berger 1988) or for climate system internal dynamics, such as pluridecadal oscillations (Mann 2007) and also for exceptional events causing dramatic changes in climate leading to drastic reshaping of soil occupation, mass extinctions etc (Whiteside and Grice 2016). Several indicators prove that we are going through a climate change at a global scale (IPCC 2013). The current debate on the issue is focused on whether the present climate change is faster than what could be expected because of 'natural' processes, whether this is causing unprecedented shifts on earth ecosystems and, more importantly, whether the anthropogenic activities are causing it. IPCC reports (IPCC 2007, IPCC 2013), as well as numerous studies (Scheffers et al. 2016, amongst others), provide convincing evidence that this is the case for the latter. Therefore, aside from designing prevention and mitigation policies, it becomes relevant to predict how earth ecosystems will respond to this accelerated climate change. This is not an easy task, because of the complexity of natural systems, having a vast number of interactions and non-linear responses that characterise their functioning. This is particularly true for marine ecosystems, which are definitely less known than terrestrial ones. This leads to a further question: do the trends observed in terrestrial systems, which are easier to observe, provide the needed conceptual schemes to predict the response of marine ecosystems to climate change?

Despite the strong interest for climate change impact on earth ecosystems and the fundamental effort carried out by the IPCC, the interaction between 'terrestrial' and 'marine' scientific communities is not frequent and the number of studies dealing

with differences between the two systems is small, if compared with the studies on individual systems.

Literature on climate change and its established or potential impacts, is incredibly vast and it is beyond the scope of this review to summarise it all. The focus of this contribution will be the differences and similarities between terrestrial and marine ecosystems that are relevant in the analysis of the response to climate change. This will aim at highlighting areas of research needing more exploration, hoping to stimulate further discussion on the topic.

## Ecosystems responses follow trajectories in a multivariate space

While our immediate perception of climate is more related to temperature and rain, all other variables, mentioned in the previous section, contribute to shape the climate. These interact via several feedbacks, involving all of them varying in time. An instantaneous set of values for these or their means and variances, would only provide partial information on how climate might affect us. A typical example is the difference between a mild continuous rain and an intense storm producing a flood, with the same total amount of water having fallen. Therefore, a more appropriate characterisation of climate would be a representation of the contemporary change of all the state variables in a multidimensional space, i.e. a phase space, which would design a trajectory. This trajectory, even if purely phenomenological, would be a much better descriptor of the climate and would be more informative of its potential impact on biota. Likewise, changes in species abundance would not fully characterise the biotic response. Their trajectory mapped in the phase space, which reflects the rates associated with their activities and the consequent interactions, would instead be the best descriptor of how the system functions (Tett et al. 2013, Crise et al. 2015). A prediction of the shape of both trajectories in the time to come is the main scope of climate studies. Due to the non-linearity of the processes in complex systems, as atmosphere and ecosystems, each point on those trajectories depends on the previous path along that trajectory, meaning that simulating changes for a sudden step-variation of state variables might not properly provide information on how the final status of the analysed system will be. We are then confronted with two problems and correspondent knowledge gaps. The first problem is to develop methods for analysing the changes along the trajectories followed by all the state variables linked to the main climate drivers which result from their mutual interactions. A similar process should also be carried out for the biotic component with the added complexity of the reciprocal feedback between biotic and abiotic processes. This approach is adopted with the so-called transient simulations to distinguish them from the equilibrium simulations (e.g. Millar et al. 2015)

The second problem relates to the biotic response which has two components which we can briefly summarise in acclimatisation and adaptation. The first is related to the tolerance of the organism to changes in environmental conditions and may involve internal biochemical adjustments up to epigenetic modifications. The second is instead

related to modifications at genomic and genetic levels. While information that relate to the first component can be generated in experimental set-ups or gathered from regular *in situ* observations, the extent and the characteristics of the second process are unpredictable. What might be within reach in the near future is an estimate of the probability of possible genomic/genetic changes building on an increased knowledge of genome dynamics, the ability to evolve and speciation rates for different class of organisms.

To overcome our knowledge gaps on many mechanisms that drive the time-dependence of the trajectories, the present approaches rely on two strategies: i. they reconstruct the trajectory by numerically simulating a reduced set of processes (e.g. Sokolov et al. 2018); ii. they mine the data with more and more advanced statistical techniques to extrapolate from present information (e.g. Sarhadi et al. 2017). However, both approaches, with their intrinsic limits, focus on the final state of the systems. Even when a reliable prediction is generated, the underlying trajectory is seldom analysed and, therefore, the complex interactions that drive the system to the final state are overlooked. In addition, transient simulations are generally carried out for one or a reduced set of forcings, for example, the progressive increase of $CO_2$. This implicitly assumes that all changes are caused by a primary driving change, the increase of temperature, which is due to the increase of $CO_2$. As discussed below, the above limitations affect our predictions of marine ecosystems more than those of terrestrial ecosystem, because of their different functioning.

## The role of the time

Those ecosystems trajectories, discussed above, develop in the phase space over time. Time is, therefore, the shared context within which all the interactions and changes take place. Time is not the driver of the changes, which depend on fluxes of matter, energy and information amongst the ecosystem components, but time is the main scaling factor which allows for characterising, quantifying and comparing the changes.

The fundamental question in ecology is how the ecosystems function or, which is substantially the same, which are their dynamics? Tracking the different states in the phase space of the ecosystems is the prerequisite for answering that question. The evolution of Man has been strongly coupled with his capability of exploiting natural resources which, even when Man was a gatherer or a hunter, had to rely on associations but also on predictions. The birth of agriculture is based on having acquired knowledge on the coupled cycles of plants and environmental forcing, i.e. on parts of ecosystem dynamics. All this leads to the essential role of ecological time series. All the present knowledge about Earth functioning is based on our reconstruction of its dynamics for the past and for the present, made possible by observations over time. Long Term Ecological Research (LTER), a very recent formalisation of a long implicitly known practice, is often perceived as a specific niche of ecological research. In fact, the only difference with any other ecological observations is the time scale, by definition longer than episodic observations focused on specific processes and, often, the sampling in a fixed, spatially limited area. Both traits often have originated criticisms, for the long term sustainability, the former and for

their representative nature, the latter. The former is more dependent on societal awareness and willing-to-support, therefore asking for an improved outreach activity. The latter, instead, can be overcome by promoting observational strategies that integrate the periodical observations with sampling efforts focused on the characterisation of the spatial context and/or on specific processes that could be revealed by periodic sampling. This can be better achieved by building networks of sites and is fundamental for directing ecological research (e.g. Vanderbilt and Gaiser 2017, Zingone et al. 2019). The discussion that follows is largely based on the information collected in observational efforts over time.

## Solid earth vs. ocean

Besides the obvious visible differences between the terrestrial and marine environments, e.g. in the first animals walk and in the second they swim, it is still an object of discussion if all the other differences prevent the identification of general ecological rules, valid for both realms. The existence of general rules in ecology, which would allow prediction of the structure of any ecosystem, once assigned initial conditions and fluxes, is part of a long lasting debate. Lawton (1999) argued against the existence of such laws, even if he admitted that macroecological patterns may display regularities beyond the ensemble of contingent events that may involve the different organisms in the ecosystem. This would imply that the final state reached after a perturbation or a transition would not be strictly dependent on the trajectory followed by the system, at least at a coarse, macro scale. This, in turn, might imply that some general structural properties, e.g. architecture of food webs or mechanisms, e.g. trophic or mutualistic interactions, should be shared by all ecosystems, independently from the components, which would be more exposed to contingent events. From this general statement, one could then assume that marine and terrestrial systems should share several common traits and that the separation by the two scientific communities is more related to tradition or differences in observation tools, than to fundamental differences in the systems (e.g. Webb 2012). However, the analysis conducted by Chase (2000) on various characteristics of the food webs in the two environments, amongst which the existence of cascades, the number of trophic levels and the dominant size of primary producers, led him to conclude that some differences, at least in the functioning and structure, exist. This would suggest that their response to climate change might also follow different paths, a possibility also discussed by him (Chase 2000).

Indeed, there are several evident differences between the two systems, especially if one compares the pelagic systems with the above-surface terrestrial ecosystems which are the most distant in terms of characteristics and are the focus of this contribution.

First of all, let us consider the dimensionality. Pelagic marine systems are fully three-dimensional and the total volume is occupied by organisms. In terrestrial systems, the third dimension has a limited thickness, with the exception of the overlying atmosphere which, however, hosts only a very small fraction of biomass (Bar-On et al. 2018). For marine organisms, this requires a significant tolerance to an extended

pressure range which is another specific trait of the marine systems. On the other hand, on land, differences in altitude may determine drastic changes in environmental conditions on short linear distances and, therefore, much sharper gradients. Another remarkable difference is the reduced gravity in the marine systems with a parallel increase in friction during movement. Energy and signal transfers are also substantially different. Light is rapidly absorbed by water and modified in its spectral properties (Kirk 2011), implying less available radiant energy and potential constraints. Light is also attenuated in the terrestrial environments but, above the surface, mostly under canopies and with a different pattern of spectral modulation (Depauw et al. 2012) On the other hand, spectral changes with depth can be a source of detectable signals by organisms (Jaubert et al. 2017). This is partially compensated by acoustic signals which propagate faster and over longer distances in the water (Hovem 2010), a fact which explains why sound and mechanical signals are widespread in marine ecosystems (Dusenbery 1992). However, there are two key differences between the two systems. One is the water availability. Water is the fundamental element of life, at least the life that we know. Terrestrial organisms rely on water supplied by precipitation or humidity in the air and in the soil while marine organisms are embedded in water, even if this means that they have to handle the osmotic pressure of the medium. The other is the medium on which organisms rely to make their life. Terrestrial systems are organised on a fixed substrate and the mobile component, the atmosphere, is where the organisms just transit to move from one fixed site to another. In the marine environment, the medium is mobile with most of the biomass living in it (Bar-On et al. 2018) and in a size range such as to make it prevalently transported by the movement.

Those differences are significant, but not all of them may directly affect the response to climate change. Some of them are crucial, i.e. temperature, water availability and medium motion, others enter the game indirectly, e.g. dimensionality, while those remaining have relevance from an evolutionary point of view but do not modify the impact of climate change on the two systems.

## Inferring and comparing potential impacts of climate change

In Table 1, the three climate components, mentioned above, are listed together with the direct dominant effect that a change in their amplitude would have on terrestrial and pelagic ecosystems. In the last row, there is an additional component, the movement of the fluid media (atmosphere and oceanic water) which is strongly intertwined with the others, in fact it depends on them, but exerts a complex, direct, very specific impact on biota.

### Temperature

Temperature is by far the most studied climate variable in terms of its impact on organisms and ecosystems. Temperature increase, or global warming, framed in the context of a rotating planet and of an active terrestrial crust, is the primary driver of all the

**Table 1.** Climate components and their direct impact on terrestrial and marine ecosystem processes.

| Change in | Impact on land | Impact in the ocean |
|---|---|---|
| Temperature | Organism metabolism | Organism metabolism |
| Precipitation | Drought | None direct |
| Cloudiness | Light availability | Light availability |
| Motion of the fluid media (atmospheric and ocean circulation) | Evapotranspiration, seeds spreading and immigration | Displacement and mixing |

other changes in climate components. Temperature is also a fundamental modulator of biotic activity and, therefore, changes in temperature produce a direct impact on organisms and ecosystems.

The reason why temperature is so important has been long known and is rooted in basic physical and chemical mechanisms. Put in a simple way, it is related to the rates by which the chemical reactions, on which organisms base their metabolism, occur and on the rates of the processes that allow the reagents involved in those reactions to meet. The reactions occurring in an organism vary from billions to trillions per second and are of several kinds. This makes it very difficult to find a universal, simple relationship between temperature and the overall biochemical functioning of an organism. However the attempts to find general patterns are numerous and are all based on the exponential dependence of chemical reaction rates on temperature and the 'activation energy', which quantifies the energy barrier that reagents need to overcome in order to lead to the products. This 'law' is generally attributed to Arrhenius (1889). Building on this and on a previous analysis by West et al. (1997) on the allometric relationship between body mass and metabolic rates (Kleiber 1932, Gillooly et al. 2001), Gillooly et al. (2001) highlighted that most metabolic reactions strongly rely on the back and forth transformation of the ADP/ATP couple, which has an activation energy of 0.65 EV and that all the activation energies are within the range of 0.2–1.2 EV. With this mechanistic model, they showed that a wide set of empirical data could be fitted by a line in a plot of the log of allometrically biomass normalised metabolic rate vs. the inverse of temperature, refining previous more empirical, similar fits. This generalisation has been actively debated within the scientific community since its first proposition (Arrhenius 1889, Gillooly et al. 2001, Clarke 2004, Clarke and Fraser 2004, Gillooly et al. 2006, amongst others). However, the acceptable correspondence between the general 'law' and the data states two important points: 1. There is an exponential increase in metabolic rates of all organisms with temperature and 2. This increase is constrained within a range which is in the order of one order of magnitude. This implies that an increase of only two degrees may increase the metabolic rate by 20–30%. However, this general rule provides only the range of variation of whole metabolic rates with temperature. As a matter of fact, when zooming in on the different components of the metabolism, differences appear. For example Alcaraz et al. (2013) showed that, for arctic zooplankton, the relationship of metabolic rates with the temperature changes depending on the considered element, e.g. phosphorus vs. nitrogen. The exponential increase in rate with temperature proceeds until the decreased performance of enzymes, the higher demand to support the higher metabolic rate etc. limits or forces it to decrease. This produces the typical bell

shaped temperature dependence of optimal metabolic activity which is organism-specific (Clarke 2017). In other words, all organisms display a temperature range of existence which clearly results from their evolutionary history and context and whose optimal range is relatively narrow. Echtoderms are obviously more exposed to external temperature changes. Additionally, on the descending side of the curve, the relationship with temperature might be process dependent. For example, Alcaraz et al. (2014) showed that carbon ingestion by and respiration of the copepod *Calanus glacialis* scale differently with temperature, thus causing a sharp discontinuity in the temperature window in which they can survive. Are these changes due to global warming having a similar impact on land and ocean? This is not the case. The heat capacity coefficient of water makes the seawater more resilient to heating, meaning that it is more difficult to produce a sudden temperature increase unless this is coupled to the dynamics of the water. On the other hand, the same heat capacity of water makes it a better medium to transfer heat from one place to another. Poloczanska et al. (2013) showed that warmer isotherms display a faster latitudinal change in the ocean than on land. In addition, Sunday et al. (2012) showed that there is a sharp difference between land and sea in the redistribution patterns of organisms, associated with isotherm migrations. On land, the poleward migration is occurring both in the leading and in the trailing part of their distribution while, in the ocean, there is no displacement on the warmer, equator-wards side. This hints at additional roles played by other components of the climate systems, like moisture and soil characteristics (Sunday et al. 2012), which have certainly greater inertia than flowing water. The bottom line is that the fluidity of marine systems favours a faster spreading of thermal changes compared to the land environment. The recent analysis by Beaugrand and Kirby (2018) is based on the assumption of a bell shaped optimal curve for each organism and, therefore, its predictions built on the decoupling between presence in the fluid and change in its temperature because of changes in heat fluxes.

However, while the annual average increase may predict coarse structural community changes to some extent, the details of changes cannot be anticipated, thus, leading back to the need for characterising the path. As an example, Maffucci et al. (2016) showed that the annual temperature increase in the Tyrrhenian Sea occurs mostly in the summer season, with winter temperatures staying within the previous range of variations. This is having a strong impact on the reproduction success of the sea turtle *Caretta caretta.* The increase in summer temperature has favoured a northwards expansion of the species while the winter temperatures that are still too cold are hampering the survival of the juveniles, thus impacting on the species recruitment.

While the response of the two systems might be different in the tempo and in the mode, there are reported cases of a significant synchronism. In a comprehensive analysis of a global regime shift in the 1980s, Reid et al. (2016) provided robust evidence of an all-encompassing impact of a rebound in global temperature after a sudden decrease following the El Chichòn eruption. This alternation of decrease-increase in temperature produced a widespread change in phenology as well as in productivity of both terrestrial and marine organisms. What remains elusive is the reason why some organisms showed more prominent responses than others, whether the amplitude of response was comparable and, if so, with which metrics a comparison would be reliable. This relates,

in my view, to the physical dynamics of the two systems which is not described by a change in the value of state variables, such as temperature.

Before analysing in more detail this important aspect of earth ecosystems, we analyse another key difference between land and ocean, that being the water availability.

## Precipitation

Water is provided to terrestrial areas by precipitations which also feed surface water networks that supply water to the more confined areas surrounding them. Roughly one quarter of the rainfall comes from the ocean but precipitation in the ocean is more than four times greater than on land (Gimeno et al. 2012). However, precipitation in the two systems has completely different impacts. On land, precipitation is a key term that rules humidity of the soil and of the atmosphere and, therefore, affects the water availability to plants and animals and impacts their physiology (Carnicer et al. 2011). By contrast and despite the fact that most of the precipitation occurs on the sea, the impact on marine organisms of fresh water added to the surface ocean is negligible, even in the case of large precipitation events. This does not mean that precipitation has no influence on marine ecosystems, but its main impact is not direct.

The increase in temperature increases the amount of water vapour in the atmosphere and, therefore, more intense precipitation events (Trenberth 2011). The poleward shift of storm track observed and predicted by existing models (Tamarin and Kaspi 2017; and references therein) will surely affect the terrestrial vegetation at mid latitudes. In general, a change in precipitation acts in quite complex ways, due also to a concurrent, anthropogenic increase of $CO_2$ in the air, which affects plant physiology. Dai et al. (2018) showed that the surface drying effect, due to Green House Gases-induced warming, dominates over the wetting effect of plants' physiology in response to increasing $CO_2$. The reduction of stomatal conductance and, therefore of evapotranspiration, caused by the increase in $CO_2$, does not mitigate surface drying. The link between warming, atmospheric moisture content, plant evapotranspiration and precipitations is one of the most important examples of feedbacks involving biota and climate and is an important term in climate simulations (Carnicer et al. 2011). This is specific for terrestrial ecosystems, even though the regulation of precipitation by marine plankton has been proposed many years ago by Charlson et al. (1987), though acting through a completely different mechanism.

Precipitation is not just liquid water. It can also fall as snow. Snow has a very important impact on the cycle of plants and animals in the terrestrial environment. In fact, the presence of snow allows the reduction of heat loss by the soil, while simultaneously providing the needed humidity to the soil. A careful analysis by Wang et al. (2018) showed how the trade-off between snow accumulation and its starting time (earlier start would increase snow accumulation) may be detrimental to the fate of plants. An example of this phenomenon can be found in the Italian Apennines, where Petriccione and Bricca (2019) showed that the reduction of snowfall, with a consequent increase in drought, had strongly impacted the community structure of plant coverage with the

disappearance of 20% of sensitive species; "a quantitative increase in more thermophilic and drought-tolerant species and a parallel decrease in more mesic, cryophilic and competitive species". Therefore, there had been an increase in diversity with a parallel extirpation of some species which did not suit the environment anymore.

This is another example of the relevance of the time course of changes. The presence of snow prevents the evaporation of water from soil whilst providing it at the time of snow melting. Its absence or even a change in the time of melting can go out of phase with the germination of some plants, thus hampering their growth. Global warming will increase the precipitation in the form of water with respect to snow. All this will impact the terrestrial ecosystems almost exclusively.

There is only one process in marine ecosystems which, even if being it is extremely weakly coupled with precipitation, shares some similarities with the effect of snow on land and this is the presence of ice. It is well known that, because of the particular properties of water, ice is colder but lighter than liquid water. This is also true when it contains a certain amount of salt. Therefore ice covers the sea surface layer as snow covers the soil. Ice cover prevents heat exchange between water and the atmosphere, thus allowing for water to remain liquid underneath. This isolating role is very similar to what the snow does for the soil.

Some species, e.g. ice diatoms or the antarctic krill *Euphausia superba,* have part of their life cycle linked to the presence of ice (Nicol 2006). If the ice does not form or melts before the time of the typical seasonal cycle, the *E. superba* life cycle is altered and, apparently, there is a higher probability that salps prevail (Atkinson et al. 2004).

It is worth mentioning that ice formation is driven only by heat fluxes, while snow presence is also driven by precipitation patterns.

## Cloudiness

Cloudiness, besides its impact on precipitation which has been discussed before, is a modulator of radiant energy reaching the earth surface. While clouds may increase the total radiation impinging on earth surface by a small amount with respect to a cloud-free sky, because of its diffuse component, the most frequent effect is to significantly reduce it by a factor that can reach 70–80% (Pfister et al. 2003). A decreasing trend in cloud coverage, even if slight, has been reported (Karlsson et al. 2017). Even though there are pluriannual trends, on average, the oscillation between brightening and dimming is more related to aerosols, often of anthropogenic origin, than to cloudiness (Wild 2009). Decrease in light intensity has an impact on photosynthetic performance of autotrophs either via preventing photoinhibition, thus improving it, or limiting the available energy in shade environments, thus reducing it. The impact of reducing or increasing light flux, which will also depend on changes in the spatial distribution of cloudiness, might have a stronger influence on the marine ecosystems because a large part of the ocean hosts a maximum of phytoplankton biomass in the subsurface layer. The Deep Chlorophyll Maximum (DCM) does not always correspond to a maximum in biomass or production, because of the rapid attenuation of light in the water col-

umn (see Cullen 2015). The dynamics of DCM are associated with the total available light coming from above, the nutrient vertical fluxes coming from below, as well as with the dynamics of the mixed layer (Letelier et al. 2004, Lavigne et al. 2015). A reduction in the available light has an impact, not only on its total production, but also on the composition of the community, i.e. on its diversity (Huisman et al. 2006) and this occurs on fairly large parts of the ocean. Interestingly, several reconstructions of past climate are based on the ratio between surface and sub-surface organism distributions, used as a proxy for mostly the stratification and mixed layer dynamics, while the cloudiness is generally neglected (e.g. Incarbona et al. 2013).

## Motion of fluid media

While the alteration of the heat budget of the Earth system is the primary driver of the climate change and also affects the elements we have briefly analysed above, the main modulators of the changes are the concurrent motions of the two fluids, the atmosphere and the oceanic water. The Earth rotation adds complexity to the non-linear interactions amongst thermal gradients, water vapour release by the ocean, soil and vegetation and, therefore, air moisture content, ultimately determining the trajectories of air transport. Likewise in the ocean, the rotation affects the paths of currents, with salinity being the additional variable instead of moisture content. The full description or a short synthesis of all the above processes is beyond the scope of this paper for its length and complexity on its own. It has to be said that ocean and atmosphere are strongly coupled and they affect each others' dynamics but the impact on biota displays significant differences in the two environments. Atmospheric transport is what determines the spatial distribution of cloud coverage, the precipitation and, partly, the horizontal heat fluxes, thus acting as a modulator of the three terms analysed above, with their different impact. It also contributes, via atmospheric deposition, to transport essential nutrients. However, the relevance of this process for the two systems is significant. As an example in the terrestrial environment, the transport of nitrogen and phosphorus has been estimated to increase the $CO_2$ removal by forests by 9% at most (Wang et al. 2017), while in the ocean, the transport of iron has been estimated to impact on $CO_2$ removal by more than 12%. The differential impact is, however, mostly on the access to the internal stocks in the two systems. Apart from the atmospheric transport, wind is a key term for vertical mixing in the ocean and therefore for the upward flux of new nutrients that drive large part of primary production in the ocean. There is no equivalent on land, where, instead, the wind is crucial for the evapotranspiration. In fact, one of the expected effects of global warming is the increase in stratification in the mid-latitudinal belt with a less effective vertical mixing even at quasi constant wind field (Doney et al. 2011). The impact is even more dramatic if possible changes in wind field are included because of their impact on the oceanic general circulation and the ice coverage (Moore et al. 2018). Growing effort is being placed on simulating all the possible effects of change in atmospheric and ocean dynamics on biogeochemical cycles, often producing contrasting scenarios. The point I want to

make here is that the 'motion of media' acts very differently in the two systems and through different mechanisms. The other difference is on the dispersal. Seed dispersal is the main mechanism for colonisation of new space by terrestrial plants. However, the timescale of this process may be long (months to years) and must cope with the previous occupation of soil. In the marine environment, dispersal not only involves the propagules of organisms, but it also transfers entire communities exposing them to a complex change in environmental conditions (Beaugrand et al. 2002) and with a large impact on the food web (Beaugrand et al. 2002, Beaugrand et al. 2003). This also has no equivalent in the terrestrial systems, especially on short timescales. This process reinforces the point that a prediction of the change must be based on the integration of the continuous change in space and time of the moving water, i.e. on an integral along the trajectory of the current.

## Is there a coupling between the two systems?

So far, I have discussed the different mechanisms by which climate acts on the marine pelagic and above-the-surface terrestrial ecosystems. However, between the two, there are no rigid barriers and one may wonder which could be, or could have been, the reciprocal feedbacks within the two sub-systems under climate forcing and the impact on biota. Indeed, if we exclude the few organisms that divide their life between solid Earth and ocean, such as, for example, some birds, a few mammals etc., the reciprocal feedback between the two systems, even when driven by biota, acts via abiotic players, i.e. the atmosphere and the water. Though, it can act on a wide range of scales up to the macroevolutionary timescale, thus being coupled with, but not necessarily driven by, climate. The iconic example is the origin of oxygenic photosynthesis which, via the accumulation of oxygen produced essentially in the marine environment (Sánchez-Baracaldo 2015, Fischer et al. 2016), also caused a drastic change in terrestrial environment and biota. More recent events, on a geological time scale, are the sapropel depositions, which are accumulations of reduced carbon in the sediments of the Mediterranean Sea (Rohling et al. 2015). Those events are driven by co-occurring processes, such as Monsoon intensification, increase in precipitation and runoff. There are several lines of evidence that the consequent increase of stratification and, possibly, the increase in export production fuelled higher nutrient inputs from land, with a parallel weakening of the thermohaline circulation in the basin and caused a decrease in oxygenation rates of the deep layer, leading to euxinia or anoxia. Any change in the hydrological cycle on land which, as discussed above, is also affected by terrestrial plants and activity, impacts, via runoff, the marginal seas and coastal areas (Meybeck et al. 2006) and can track climate fluctuations via the paleobiological changes and their isotopic signatures (e.g. Sprovieri et al. 2012). A third example is the observed increase in iron transport from land during glacial times initially hypothesised by Martin (1990). The harsher climate on land during those periods eventually produced an increase in iron transport to the ocean with a parallel increase in carbon vertical export and, very likely, a change in community structure. The impact of the recorded increase in iron transport to the

ocean is still at the centre of an intense debate, but the evidence supporting the coupling between changes induced on terrestrial environment on land and those in the marine ecosystem is definitely robust. A very crude generalisation would be to separate the scales. At the interface between land and sea, i.e. on a small scale, climate change on land would act via runs-off and would be more frequent from the land to the sea, even though it can be hypothesised that habitat destruction on the near-shore due to storm intensification might impact on on-shore habitats. On a larger scale, the atmosphere would likely play a prominent role, also via global biogeochemistry.

## What knowledge gaps do we have to fill and how could they be filled?

We discussed above that temperature changes play a role at multiple levels. Prediction of temperature future trends is still a great challenge for Earth system models (Bonan and Doney 2018) due also to the feedback of biota. This in turn depends on their physiological fitness, as well as on their capabilities for acclimatisation and, eventually, modification of their fitness via mutation. The importance of biota feedback can be generalised to many more processes and is the key challenge that the scientific community will face in the near future. This can only be obtained via a holistic approach that should merge classical observational methods with the recently developed new tools, such as bio-optics, bio-acoustics and -omics (Karsenti et al. 2011, Coles et al. 2017, Crise et al. 2018, amongst others). It should consider in more detail the multiple interactions occurring within communities which are differently modulated in the marine and terrestrial environments and display plasticity and complex outcomes (Tylianakis et al. 2008, D'Alelio et al. 2016, amongst others). It should be continued in time as the LTER community is showing for many years. In fact, most of the issues discussed in this paper were stimulated by the observations conducted over the last decades at the LTER station MC in the bay of Napoli (Zingone et al. 2019). This information, especially if integrated with modern techniques and approaches, especially those based on bioptical and molecular methods, can feed a new generation of models (Coles et al. 2017, Stec et al. 2017, D'Alelio et al. 2019).

We are facing a faster change in the environment even with regards to climate because of anthropogenic actions. We know from the past that climate change induces ecosystem changes. However, our data result from a natural filtering process that transmits only the prominent changes. The importance of 'history' has been stressed before. In the background section, I raised the question on why biota respond to changes in environmental conditions that are often smaller than the variations they experience in one single year. I believe that this too is related to the time course of the change. Short term fluctuations are tolerated by organisms which, in addition, tune their life cycles to the most suited conditions for them, meaning that many of them do not experience the whole range of variations of the seasonal cycle or adopt different solutions to cope with it. Besides the cycle of illumination which is the same for the ocean and the land, terrestrial ecosystems experience a more fluctuating environment with wider ranges of variations for the key climatic components. While the heat capacity of seawater buffers the temperature, an equivalent buffering role is partially played by the soil with

respect to water availability. On the other hand, the real modulating player is the motion of the medium, on land because of the impact of wind in moisture transport and evaporation and evapotranspiration and in the ocean because of the currents. The main difference is that, on land, the inertia is much higher because the motion of medium changes the conditions but does not move the organisms, whereas in the ocean, organisms in many cases move with the water. Nectonic organisms are in-between because they may move independently from the medium, to some extent. This does not always mean that they can escape the impact of changes, because a moving environment also changes their environment.

In any case, the conceptual framework for the two systems has some relevant differences and even if one wants to build on unifying theories, the real impact must be based on the integral of the changes over time which depends on different processes on land and in ocean.

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